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Invited review

Do managed bees drive parasite spread and emergence in wild bees?

Peter Graystock [a, *], Edward J. Blane [b], Quinn S. McFrederick [a], Dave Goulson [c], William O.H. Hughes [c]

[a] Department of Entomology, University of California, Riverside, CA 92507, USA
[b] Natural England, Mail Hub Block B, Whittington Road, Worcester, WR5 2LQ, UK
[c] School of Life Sciences, University of Sussex, Brighton, BN1 9QG, UK

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ABSTRACT

Bees have been managed and utilised for honey production for centuries and, more recently, pollination services. Since the mid 20th Century, the use and production of managed bees has intensified with hundreds of thousands of hives being moved across countries and around the globe on an annual basis. However, the introduction of unnaturally high densities of bees to areas could have adverse effects. Importation and deployment of managed honey bee and bumblebees may be responsible for parasite introductions or a change in the dynamics of native parasites that ultimately increases disease prevalence in wild bees. Here we review the domestication and deployment of managed bees and explain the evidence for the role of managed bees in causing adverse effects on the health of wild bees. Correlations with the use of managed bees and decreases in wild bee health from territories across the globe are discussed along with suggestions to mitigate further health reductions in wild bees.

Contents

* Corresponding author.
E-mail address: peter@graystock.info (P. Graystock).

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1. Introduction

Growing demand for food and agricultural intensification is resulting in a growing demand for pollination services and, ironically, growing pressures on wild bees. Currently both managed and wild pollinators are suffering alarming declines in many parts of the world (Potts et al., 2010). In the last century, many wild bee populations have become reduced and fragmented, and with reduced genetic diversity are now facing increased vulnerability to infectious diseases and other stressors such as pesticides and reduced resources (McCallum and Dobson, 2002; Tarpy, 2003; Whitehorn et al., 2011). Over 25% of wild bees in Belgium and 47% of native bumblebee species in Hungary have exhibited recent declines (Sárospataki et al., 2005). Similar declines in wild pollinators are found in Britain, Ireland, Spain, France, Morocco, Corsica, Tibet, Brazil and Madagascar (Fitzpatrick et al., 2007; Kosior et al., 2007; Martins and Melo, 2010; Rasmont et al., 2005; Williams, 1982; Xie et al., 2008). In the North American mid-west, half of the native bumblebee species have declined during the mid-twentieth century (Grixti et al., 2009), while bumblebees have also declined in diversity, evenness and abundance in eastern North America between 1971 and 2006 (Colla and Packer, 2008). Today 11% of all bumblebee species worldwide are listed as threatened in the IUCN Red list (Williams and Osborne, 2009).

Emergent infectious diseases (EIDs) are ranked as one of the top five causes of species extinction worldwide (Daszak et al., 2000). They are defined broadly as diseases that have recently increased in either incidence, demographic or host range, or that have recently evolved or been discovered (Daszak et al., 2001, 2000; Lederberg et al., 1992; Morse, 1993). Many instances of EIDs in wild animals are the result of interactions with domesticated/managed species (Fig. 1). One of the main conservation concerns regarding the use, and particularly the importation, of managed bees, is that of exotic parasite (or parasite strain) introduction and subsequent spillover to wild populations (Blitzer et al., 2012; Goulson et al., 2008). By allowing managed and/or imported bees to mix with wild pollinators, there is the potential for disease emergence via direct transmission and facilitated by changes in host susceptibility.

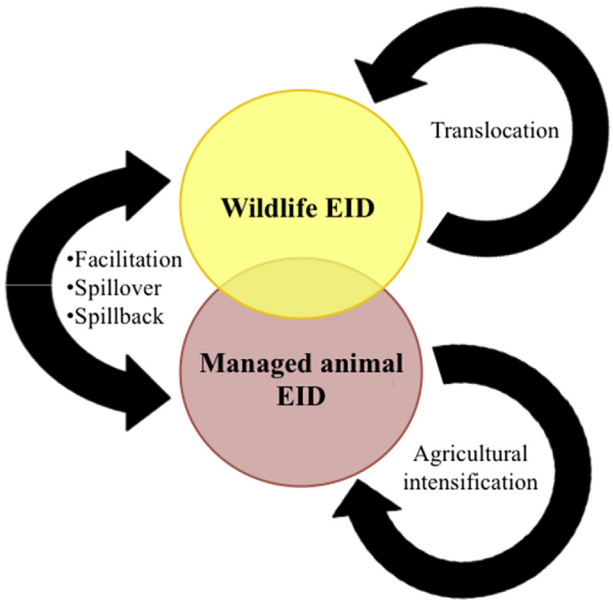

Fig. 1. The key factors that may drive disease emergence within and between populations of managed and wild bees. Adapted from Daszak et al. (2000).

2. Parasite facilitation

As with other animals, bee susceptibility and subsequent pathology is often increased when individuals are stressed (Freestone et al., 2008; Jokela et al., 2005; MacKinnon, 1998; Møller et al., 1998). Dense populations of managed bees can cause stress to wild populations and have been linked to developmental retardation in wild bees (Elbgami et al., 2014; Goulson and Sparrow, 2008; Thomson, 2004). It's also likely that, as in other organisms, such competitive and nutritional stresses can influence their susceptibility to infection (Brown et al., 2003; Graystock et al., 2014; Hedtke et al., 2011; MacKinnon, 1998). This stress would therefore facilitate an increase in prevalence or intensity of natural parasite infections in wild bees, independent of any transmission between the two groups of bees.

3. Parasite spillover

Parasite spillover occurs when the reservoir population (usually managed stock) transmit disease to the sink (in this case, wild) population (Daszak et al., 2000; Fig. 2). Emergence of the parasite in wild populations may be self-supporting or may require continued mixing with the source/reservoir population. When intra-specific and/or inter-specific transmission rates are low, infection of susceptible individuals may occur in many instances without the parasite establishing in the wild population (Hatcher and Dunn, 2011). Closely related, sympatric hosts have a greater potential to transmit pathogens between them, though the virulence of the parasite may differ (Graystock et al., 2013a; Perlman and Jaenike, 2003; Schmid-Hempel, 2011).

4. Parasite spillback

In parasite spillback, a natural parasite infection in the wild host population transmits to the managed host population, increases in prevalence within it, and then spills back into the wild population, resulting in an increase in prevalence in wild populations (Hatcher and Dunn, 2011; Kelly et al., 2009; Fig. 2). Here, the newly infected animals may achieve unnaturally high parasite prevalence due to their high density (for example, honey bee colonies in apiaries are much denser than in wild honey bee populations). This unnaturally high parasite prevalence then spills back, driving parasite levels in the wild population higher than would naturally occur (Hatcher and Dunn, 2011; Kelly et al., 2009). Another factor in spillback from managed populations is that well managed, healthy animals may be able to tolerate pathogenic effects better than wild hosts. Such tolerance may result in a population of asymptomatic, yet infectious, managed bees.

5. Is spillover/spillback between wild and managed bees common?

Over the past century there have been huge advancements in agricultural intensification, combined with a rapid global demand for food (Aizen and Harder, 2009; Aizen et al., 2009; Gallai et al., 2009; Velthuis, 2002). One of the advances farmers increasingly utilise is the purchase of pollination services via managed honey bees or managed bumblebee colonies (VanEngelsdorp and Meixner, 2010; Velthuis and Van Doorn, 2006). The practices and regulations in place for managed bee use are not uniform across the globe and there is growing concern that managed bees may pose a disease risk to other pollinators (Goulson and Hughes, 2015; Graystock et al., 2014; Meeus et al., 2011). Here we review the domestication of bumblebees and honey bees before looking at specific examples from across the world where parasite

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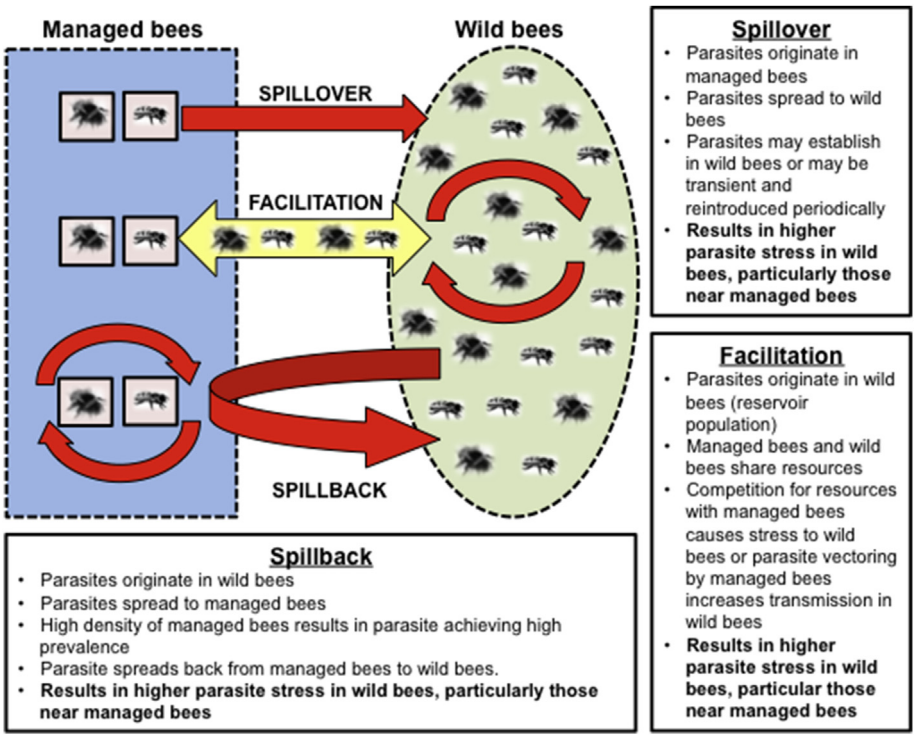

Fig. 2. Highlighting the three main mechanisms that influence parasite infections between managed and wild bee populations. Arrows represent direction of potential parasite spread as a result of the mechanism.

transmission is reported to have occurred following the use of managed bees for crop pollination. Finally, we consider the parasite threat that managed honey bees or managed bumblebees may pose to wild bees, highlighting ways to reduce this threat and possible avenues for further research.

6. Success and domestication of pollinators

In Europe, the yields of 84% of 264 crop species rely on, or are improved by insect pollination (Klein et al., 2007; Williams, 1994). Modern farming is increasingly intensive, creating large areas with limited proximity to pollinator-rich areas such as wild meadows or hedgerows. When flowering crops are used in such fields, they can suffer from suboptimal crop production due to the fields and surrounding area providing few or no habitat for pollinators such as bumblebees to nest (Free and Williams, 2009; Kremen et al., 2002). Additionally, areas can be planted in such densities that wild pollinator populations are unable to service all crops. To increase crop yields, it is therefore beneficial to boost pollinators numbers by utilizing managed bees (Lye et al., 2011a). Honey bees (*Apis*) and bumblebees (*Bombus*) are the two groups of bees which have been most successfully domesticated and used in crop pollination (VanEngelsdorp and Meixner, 2010; Velthuis, 2002).

7. Honey bee domestication

Out of about 20,000 known bee species only 7 of these are honey bees (Arias and Sheppard, 2005; Engel, 1999; Koeniger and Koeniger, 2000). All but one honey bee species occur only in Asia, while the other, *Apis mellifera*, has a natural range from central Asia into Europe and Africa (Ruttner, 1988; Seeley, 1985; Sheppard and Meixner, 2003). Managed for their honey since at least 2600 BC, the economic value of honeybees has ensured their translocation along with every large-scale human migration (Crane, 1999, 1975; Ransome, 2004; VanEngelsdorp and Meixner, 2010). This movement across the world has caused some conservation concerns; the introduction of managed honey bees has been found to cause changes in seed set of natural floral and reduce the fitness of native pollinators (Goulson and Derwent, 2004; Goulson and Sparrow, 2008; Goulson, 2003; Huryn, 1997). Despite these concerns, *A. mellifera* is now the most commonly managed pollinator and is found in nearly all habitable regions (Engel, 1999; Ransome, 2004; VanEngelsdorp and Meixner, 2010). Fifty-two of the top 115 global food commodities depend on honey bee pollination for either fruit or seed set (Klein et al., 2007), with honey bees being capable of increasing the yields of 96% of animal-pollinated crops, making them the most important pollinator for most crops worldwide (Delaplane et al., 2000; Klein et al., 2007; McGregor, 1976). Recently it has been estimated that projected honey bee populations will not be able to satisfy agricultural pollination demands in the future (Aizen and Harder, 2009).

8. Bumblebee domestication

For many wildflowers and valuable crops such as raspberry and tomatoes, honey bees are inefficient pollinators (Batra, 1995; Cane, 2005; Greenleaf and Kremen, 2006; Velthuis and Van Doorn, 2006). Bumblebees have several adaptations such as the ability to buzz pollinate (sonication) and their insulated bodies making them ideal pollinators for these plant and crop species (De Luca et al., 2013; Goulson, 2010; Heinrich, 1993; Velthuis and Van Doorn, 2006). Unlike honey bees, bumblebees do not produce honey or hive material suitable for mass market sales. Their commercial use is purely based on demand for their pollination services where honey bees are not the most efficient pollinator (VanEngelsdorp and Meixner, 2010).

Prior to bumblebee domestication, crops requiring sonication such as tomatoes were mechanically vibrated to achieve

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pollination. The cost of mechanically vibrating the plants was over €10,000 per ha per year in 1988 (Velthuis and Van Doorn, 2006). Like honey bees, bumblebees have more recently been translocated by humans to aid crop production, even before their true 'domestication'. Between 1882 and 1906, hundreds of bumblebee queens were translocated from the UK to New Zealand to establish wild colonies and improve the seed set of red clover, with four UK species (*Bombus hortorum*, *Bombus ruderatus*, *Bombus subterraneus* and *Bombus terrestris*) all becoming naturalised in New Zealand as a result (Hopkins, 1914; Lye et al., 2011b). Following this agricultural success in New Zealand, *B. ruderatus* queens from the naturalised New Zealand stock were translocated to Chile for their red clover pollination in 1982 and 1983 (Arretz and Macfarlane, 1986).

By the 1960's there was a clear demand to utilise bumblebees as pollinators on an intensive scale, which motivated their domestication (Free, 1970; Holm, 1966; Velthuis and Van Doorn, 2006; Velthuis, 2002). Unlike honey bees, bumblebees require diapause initiation after mating and then need to be stimulated to lay eggs following emergence (Goulson, 2010). Various protocols were developed to achieve this, such as the inclusion of honey bee workers to stimulate egg laying by bumblebee queens (Heemert et al., 1990; Ptacek, 1985; Van der Eijnde, 1990). By the late 1970's enough progress had been made to fully domesticate the most common European bumblebee species, *B. terrestris* (Röseler, 1977; Velthuis and Van Doorn, 2006). With the joining of both demand and technology, commercial production of bumblebee colonies began in 1987 and by 1989 three companies based in Belgium and the Netherlands had begun production (Velthuis and Van Doorn, 2006). This growing industry was estimated to be worth in excess of €55 million pa in 2006 and is served by over 30 factories (Velthuis and Van Doorn, 2006). Globally, over two million bumblebee colonies are reared and transported to various countries for farm placement. Placement of hives in fields are recommended to be at near natural densities of 1 per km^2 but farmers frequently buy more and site them in vertical 'stacks' creating zones of incredibly high density (6 colonies in 1 m^2). Although the most utilised species in commercial colonies is *B. terrestris*, several others have been domesticated/managed including *Bombus lucorum*, *Bombus occidentalis*, *Bombus ignitus*, *Bombus canariensis* and *Bombus impatiens* (Asada and Ono, 1997; Velthuis and Van Doorn, 2006; Wu, 2008). This diversity is an attempt to mitigate environmental damage from the escape of exotic pollinators by the production of native stock for various countries (Dafni et al., 2010; Velthuis and Van Doorn, 2006), although non-native species or subspecies are still used in many instances (Velthuis and Van Doorn, 2006). In order to produce enough bumblebee colonies commercially to meet worldwide demand, it is estimated that around 500 tonnes of pollen is required to feed the colonies in the rearing facilities (Goulson, 2013). This pollen is harvested by honey bees and collected from their pollen baskets using 'pollen traps'. The bumblebee industry is therefore reliant on the honeybee market with Spain and China being be key suppliers of pollen (Centre for the Promotion of Imports from developing countries, 2009).

9. Reports of possible spillover from managed bumblebee or honey bee populations

While this review is focused on the parasite threats from managed bees, other concerns have also been raised over the use of managed bees including non-native naturalisation, competition and changes in floral seed set (Goulson, 2003; Goulson et al., 2002; Ings et al., 2006; Kremen et al., 2002). Many of these other threats can be exacerbated by parasite emergence (Daszak and Cunningham, 1999; Jones et al., 2008). When considering the parasite risks that managed bees pose to wild bees, it is important to note that spillover can act in either direction since both managed and native populations can act as a parasite reservoir. Transmission between different managed species could then allow unexpected parasites to spillover to wild bees (Graystock et al., 2013a; McMahon et al., 2015). In cases where parasites from wild bees transmit to managed bees, it is important to also look for signs of possible spillback (Kelly et al., 2009). To identify spillover and spillback, studies must account for: 1) whether pathogens have emerged in tandem with managed bee introduction, 2) if the dynamics of pathogen spread indicate that the health of wild bees near managed bees is different from areas without managed bees, and 3) ideally trace pathogen origin with genetic markers (Daszak et al., 2000; Kelly et al., 2009; Power and Mitchell, 2004; Wood et al., 2012). Frequently all three are lacking so identification of the type of parasite dynamics occurring cannot be fully reconciled. Despite this, the balance of evidence on a case-by-case basis can allow for a reasonable verdict. On this premise, evidence for managed bees causing harm to wild bees is presented below as a series of case studies.

9.1. Case study 1: transmission between managed and wild honey bees globally

The transmission of parasites to the European honey bee from their original host, the Asian honey bee, led to some of the most dramatic honey bee declines in recorded history. Two parasites are particularly noteworthy: the ectoparasitic *Varroa* mite, and the microsporidian *Nosema ceranae* (Chauzat et al., 2010; Neumann and Carreck, 2010; vanEngelsdorp et al., 2011).

Varroa: The ectoparasitic mite *Varroa jacobsoni* is native to Eastern Asia where it parasitizes Asian honey bees such as *Apis ceranae* (Oldroyd, 1999; Oudemans, 1904). Some time in the mid 20th century, *Varroa* spilled over from its natural host to managed colonies of *A. mellifera* that had been transported into Asia by apiculturists for honey production and pollination services (Rosenkranz et al., 2010). This host jump, determined by genetic changes in the *Varroa* population, resulted in a new species, *Varroa destructor* (Anderson and Trueman, 2000; Dietemann et al., 2012; Solignac et al., 2005). This occurred on a large scale at least twice, forming the Japanese and Korean strains (Anderson and Trueman, 2000). The first wave of infection started by *Varroa* jumping from *Apis cerana* to *A. mellifera* in Japan in 1957 then spreading on to Paraguay in 1971, Brazil in 1972 and then within the decade on to North America (Jong et al., 1982; Sakai and Okada, 1974; Solignac et al., 2005). The second wave of infection occurred when *Varroa* jumped from *A. cerana* to *A. mellifera* in the region of Primorsky Krai, Russia, then spread through the *A. mellifera* populations in Europe before being recognised as a globally emerging parasite (Crane, 1978; Solignac et al., 2005). This rapid spread was made possible by the transport of managed bees across countries and between continents, allowing *Varroa* mites from infested hives to spillover to new hives in new areas (Boecking and Genersch, 2008; Bowen-Walker et al., 1999; Solignac et al., 2005).

Following their spillover to *A. mellifera*, dramatic honey bee declines were reported in both managed and wild colonies with a host of symptoms resulting from infestation (Carreck et al., 2002; Le Conte et al., 2010; Martin et al., 2012). Honey bees from *Varroa* infected colonies are smaller and become cognitively impaired (Kralj and Fuchs, 2006; Kralj et al., 2007; Rosenkranz et al., 2010), their hives produce less honey (Emsen et al., 2013), and only survive 2–3 years (Fries et al., 2006a; Korpela et al., 1993). *Varroa* mites feed off the hemolymph of host bees, and are therefore excellent vectors of virus parasites. This direct injection of virus into the haemolymph of the host results in more intense infections with pathogenic effects, known as Varroosis (Boecking and Genersch,

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2008; Dainat et al., 2012). While good bee husbandry can help reduce colony losses, the *Varroa* mite is now considered to be a significant contributor to *A. mellifera* losses worldwide, particularly of feral and wild honey bee populations which in the USA and Europe are thought to have been significantly reduced following the emergence of *Varroa* (Martin et al., 2012; Pohorecka et al., 2011). In the UK mainland and parts of Europe, its believed that *Varroa* aided declines have resulted in the loss of truly wild populations of *A. mellifera*, with only feral colonies left (Jaffé et al., 2010; Moritz et al., 2007; Thompson et al., 2014).

Nosema ceranae: It is believed that the microsporidian *Nosema ceranae* was first detected in the Asian honey bee, *Apis ceranae*, in 1975, although earlier misidentifications may have occurred (Fries et al., 2006b; Singh, 1975). It was only in 1996 that it was formally described as *N. ceranae* (initially misidentified as *Nosema apis*), from samples of managed *A. cerana* in China (Fries, 2010; Fries et al., 1996). Cross-infectivity experiments showed *N. ceranae* to be infective to the European honey bee *A. mellifera* as well as its natural host (Fries, 1997). Symptoms of *N. ceranae* infections have been termed Nosemosis type C. They are stronger in younger bees, and include suppressed immune function, increased hunger and increased mortality, causing *N. ceranae* to be considered a contributing factor to colony losses in some, but not all, areas (Antúnez et al., 2009; Higes et al., 2010; Mayack and Naug, 2009; Roberts and Hughes, 2014).

In 2005, samples of *A. mellifera* from an apiary in Taiwan that also housed *A. cerana* honey bees were found to be infected with *N. ceranae*, suggesting spillover from its natural host could be occurring (Huang et al., 2007). This was also confirmed in Europe when *N. ceranae* was found in an *A. mellifera* apiary in Spain (Higes et al., 2006). Historical bee samples have shown *N. ceranae* started to spillover to *A. mellifera* earlier than this but an exact date is not yet resolved (Fries, 2010). It has been detected in *A. mellifera* collected before 1990 in Uruguay (Invernizzi et al., 2009), in North America from 1995 (Chen et al., 2008), and in Spain from 2000 (Botías et al., 2012). Temporal analysis shows that *N. ceranae* introduction, spread and prevalence has increased over time (Klee et al., 2007; Paxton et al., 2007). Today, *N. ceranae* is present on all continents where *A. mellifera* is present and has been found at similar prevalence in managed and nearby wild honey bees (Giersch et al., 2009; Klee et al., 2007; Thompson et al., 2014).

9.2. Case study 2: transmission between managed and wild bumblebees in Japan

The first reported instance of pathogen transmission between commercially reared bumblebees and wild bumblebees was in Japan. Commercial *B. terrestris* have been imported into Japan primarily for tomato production since 1991 (Goka et al., 2001). Within a decade, over 40,000 colonies of non-native *B. terrestris* were being imported annually into Japan from Europe (Velthuis and Van Doorn, 2006). On average, 20% of the commercially produced colonies of *B. terrestris* examined were found to be infected with the European strain of the tracheal mite *Locustacarus buchneri* (Goka et al., 2001, 2000). In a separate study, a viable microsporidian parasite (resembling *N. bombi*) was also detected in a commercially produced *B. terrestris* colony imported into Japan (Niwa et al., 2004). At the same time, a number of bumblebee species native to Japan, including *B. ignitus*, were taken back to Europe in an attempt to commercialise them. This process carried the risk of European parasites, such as *L. buchneri*, infecting the Japanese bumblebees in the production facilities and then being carried back with them into Japan.

High mite incidence in managed bumblebee colonies is a particular concern as the mite feeds, reproduces, and lives inside the abdominal air sacks (trachea) of female bumblebees (Yoneda et al., 2008). Heavily infected bumblebees suffer from diarrhoea and lethargy, stop foraging, and have a reduced lifespan, thus retarding colony growth (Husband and Sinha, 1970; Otterstatter and Whidden, 2004). This reduces the ability of the commercially produced bumblebees to pollinate the intended crops efficiently and it could negatively impact wild bumblebees if spillover was to occur. Due to this concern, between 1997 and 1999 three native bumblebee species, *Bombus hypocrita sapporoensis*, *B. hypocrita hypocrita* and *B. ignitus*, were screened across Japan with 8%, 1% and 0% respectively being found to be infected with the mite (Goka et al., 2001). Molecular analysis suggested that spillover of *L. buchneri* from managed bumblebees to wild bumblebees had not at that time occurred. However, the fact that 20% and 17% of commercially produced *B. terrestris* and *B. ignitus* respectively were infected with the mite, together with the escape and naturalisation of commercially produced *B. terrestris* in Japan, and the finding that the European haplotype of *L. buchneri* was able to parasitize the native *B. ignitus*, suggested that the potential for spillover from bumblebees imported into Japan was high (Goka et al., 2001; Kondo et al., 2009). A similar study, run between 2000 and 2001 found wild *B. hypocrita* bumblebees infected with European mites, while and commercially produced bumblebees were infected Japanese mites, showing that spillover had occurred in both directions (Goka et al., 2006). By 2001, commercially produced bumblebees were no longer found to have *L. buchneri* infections and there are no subsequent reports of *L. buchneri* in commercially produced bumblebees in Japan. Studies in Poland also determined commercial bumblebees to be free from mites now, however a recent study did find them in south America (Reade et al., 2014; Rożej et al., 2012; Sachman-Ruiz et al., 2015). The more rigorous, and apparently successful, control of the mite in stocks exported to Japan was however, too late to prevent the spillover of the parasite into Japan (Goka et al., 2006). It is not known whether there are still mites of European descent circulating in wild bumblebees in Japan, or if the spillover was transient and dependent on continued introduction from managed bees.

9.3. Case study 3: transmission between managed and wild bumblebees in North America

In 1992, the Animal and Plant Health Inspection Service (APHIS) in North America granted a permit for the importation of native bumblebees *B. occidentalis* and *B. impatiens* from Europe (Wehling and Flanders, 2005). These North American bees had been reared in European facilities along with European *B. terrestris* and likely fed pollen collected from European honey bees (Velthuis and Van Doorn, 2006; Winter et al., 2006). While their importation back into North America was under condition of parasite screening, the methods used had limited sensitivity (Ghosh and Weiss, 2009; Klee et al., 2006; Ndao, 2009; Procop, 2007; Rinder et al., 1998; Yang and Rothman, 2004). Following concerns from conservationists, importation was stopped and the use of *B. occidentalis* was restricted to its native range in Western North America, with the use of *B. impatiens* being restricted to its range in Eastern North America (Wehling and Flanders, 2005). As a result, breeding lines of both species were maintained together in new facilities in Canada and the United States.

In 1997, *B. occidentalis* bumblebees in production factories in California started suffering from high levels of the microsporidian parasite *Nosema bombi* and stocks plummeted (Wehling and Flanders, 2005). This coincided with unusually high incidences of *N. bombi* in some wild bumblebee populations in North America and rapid declines in some species (including *Bombus affinis*, *B. occidentalis*, *B, pensylvanicus* and *Bombus terricola*; Flanders et al.,

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2003; Thorp, 2005; Thorp and Shepherd, 2005; Winter et al., 2006). Bumblebees infected by *Nosema bombi* can become sluggish, have increased mortality, reduced egg production, and infected colonies tend to be smaller and produce fewer reproductives (Fantham and Porter, 1914; Otti and Schmid-Hempel, 2008, 2007; Rutrecht and Brown, 2008; Schmid-Hempel and Loosli, 1998; Van der Steen, 2008; Whittington and Winston, 2003). Molecular analysis on a small number of samples suggested that *N. bombi* found in declining wild bumblebees may have been from a recent introduction, suggesting its emergence via importation with commercially reared bumblebees (Cameron et al., 2011; Winter et al., 2006). The concurrent timing of the declines of the wild and managed bumblebee populations in North America is suggestive of the same factor being involved, with *N. bombi* then being the best candidate.

This evidence, however, is only correlational. *N. bombi* is known to have been present in North American bumblebees prior to the introduction of commercially produced bumblebees, and recent molecular analysis suggests isolates of *N. bombi* with both American and European origin may exist in North American bumblebee species (Cordes et al., 2012). Declining populations can be more prone to parasite infections, so cause and effect cannot always be clearly disentangled on the basis of correlational data alone (Brown, 2011). Alternatives to the spillover of European *N. bombi* into North American bumblebees are for American *N. bombi* to have spilled over into commercially produced bumblebees and then spilled back into wild bumblebees, or for the use of commercially produced bumblebees to have facilitated an increase in *N. bombi* levels in wild bumblebees due to increased competitive stress or parasite vectoring, or for levels in managed and wild bumblebees to have increased independently due to some other causal factor(s). Two later studies found that the prevalence of infections with the *N. bombi* and *Crithidia bombi* parasites was higher in wild bumblebees caught near sites using commercially produced bumblebees than in wild bees caught 2 km or further from such sites (Colla et al., 2006; Otterstatter and Thomson, 2008), suggesting that spillover, spillback or facilitation was occurring. A further meta-analysis of all possible causes of bumblebee declines in North America found that the declines of *B. terricola* and *Bombus pensylvanicus*, but not *B. affinis*, were associated with the use of commercially produced bumblebees, making them the most probable cause for the declines of these species (Szabo et al., 2012).

In addition, in recent years there are several reports of managed bumblebees delivered to North America, being found with parasites including *L. buchneri*, *N. bombi*, *Apicystis bombi* and the viral pathogens deformed wing virus (DWV), black queen cell virus (BQCV), Israeli acute paralysis virus (IAPV), Chronic bee paralysis virus, and Kashmir bee virus (Sachman-Ruiz et al., 2015). The presence of these parasites upon delivery carries with it the potential for disease emergence and spillover with any interacting wild bees in the area.

9.4. Case study 4: transmission between managed and wild bumblebees in the United Kingdom and Ireland

Managed *B. terrestris dalmatinus*/*terrestris* started being imported into the British Isles from Europe in 1989 (Ings et al., 2006; Velthuis and Van Doorn, 2006). In 2008, 74% of 68 (as yet unopened) commercially produced *B. terrestris* colonies examined (imported from two different suppliers) were found to be infected with either *C. bombi*, *N. bombi*, or *A. bombi* (Murray et al., 2013). In addition, bumblebees captured at six sites in Ireland with a history of using managed bumblebees were found to have elevated levels of parasite infection (Murray et al., 2013). The presence of parasites in hives upon delivery plus the increased prevalence of those parasites in conspecifics suggests parasite spillover taking place in Eastern Ireland (Murray et al., 2013). In 2010, following a clarification of section 14 of the Wildlife and Countryside Act 1981, the release of non-native bumblebees subspecies required a release licence that was only issued if the bees were 'disease-free'. This screening of the bees was self-regulated by the producers in accordance with the Natural England licence conditions (Central Office of Information, 2009; Natural England, 2009). These conditions initially required stocks in the rearing facilities to adhere to a minimum of microscopy screening for *A. bombi*, *C. bombi*, and *N. bombi* of 2 workers from each 200 colonies every 10 weeks, with a minimum sample size of over 2000 per year. On the same sample size, bees were visually inspected for wing deformities and newly collected queens were to be visually screened for *Sphaerularia bombi*. In addition, at least routine visual inspection was required for *L. buchneri* (following dissection under binocular microscope), *Melittobia acasta* and small hive beetle (Natural England licencing conditions NNR/2007/30-33). Although not the most sensitive screening methods, the breadth of parasites screened for, particularly those specific to bumblebees was far superior to the honey bee-centric conditions of the European directive 92/65/EEC on imports.

By 2010, the screening requirements of non-native subspecies imports were somewhat undermined when commercial bumblebee breeders began importing the native subspecies *B. t. audax* into the UK from rearing facilities in continental Europe. This had been done to meet concerns from Natural England about the release of non-native bees. However, The regulating body for non-native animal releases in England, Natural England, can only enforce licence requirements for use of non-native bees and so the release of *B. t. audax* is largely unregulated. In 2010, no difference in the prevalence of *C. bombi* was found between wild bumblebees collected near farms using or not using commercially produced bumblebees, although the parasite did increase in prevalence during the summer only at sites using commercially produced bumblebees which could suggest spillback (Whitehorn et al., 2013). In 2011, wild bumblebees from around farms in England using commercially produced bumblebees were more likely to be infected with the parasites *A. bombi*, *C. bombi*, and *N. ceranae* than wild bumblebees near farms not using managed bumblebees (Graystock et al., 2014). *Nosema ceranae* was first detected in bumblebees in Argentina is believed to have spilled over from honey bees (Plischuk et al., 2009). Its effects on bumblebee fitness are still unclear. Initial descriptions detected damaged epithelial cells suggesting spore production in the gut (Plischuk et al., 2009). In one study, controlled inoculations of mixed-aged *B. terrestris* workers with *N. ceranae* confirmed infection and spore production, and found reduced host survival over a 14 day period (Graystock et al., 2013a). In another study, inoculations of 2 day old *B. terrestris* workers produced persistent infections over a 21 day period, but survival was not reduced (Fürst et al., 2014). In 2011, 2012, screening on arrival of 48 commercially produced *B. terrestris* colonies from 3 different suppliers found that 77% of colonies contained bees with at least one parasite species known to harm bumblebees or honey bees, including *A. bombi*, *C. bombi*, *N. ceranae*, DWV, *Nosema apis* and *N. bombi*, with several of these being confirmed experimentally as being infectious (Graystock et al., 2013b). The following year, Natural England tightened up the release regulations on non-native bumblebees while a thorough review of the threats was conducted (Natural England, 2012, 2009). During this time, suppliers were requested to use molecular methods to screen for the bumblebee parasites *N. bombi*, *C. bombi*, *A. bombi*, plus the traditionally termed honey bee parasites *N. apis*, *N. ceranae*, and DWV. An updated risk assessment on *B. terrestris* was carried out on behalf of the UK Non-Native Species Secretariat, which highlighted the risks of establishment and hybridisation with native *B. t. audax*. As a result, Natural England heavily

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restricted the release of non-native *B. terrestris*, with the 2015 licence only permitting this if commercial stocks of *B. t. audax* were unattainable. Native stocks of *B. t. audax* are still permitted for release to the UK despite them having previously been found to be equally as likely to be infected as *B. t. dalmatinus*/*terrestris* (Graystock et al., 2013b). This is of huge concern since the subspecies now being released into the UK has no legal requirement for disease screening or escape proofing whatsoever (apart from the honey bee centric restrictions relating to importation) (Graystock et al., 2013b). This is likely to remain the case unless local licencing is changed to allow the native sub species to be regulated (via its addition to schedule 9 and 14ZA of the Wildlife and Countryside Act), or European licencing is changed to encompass the breadth (and sometimes asymptomatic) nature of harmful parasites found in bumblebees.

9.5. Case study 5: transmission between managed honey bees and wild bumblebees in Europe

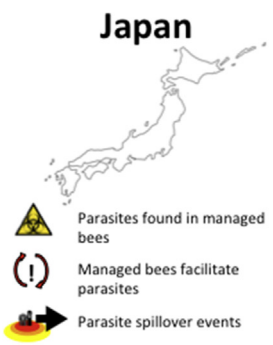
In 2004 10% of commercially reared bumblebee queens inspected had the symptoms of deformed wing virus (DWV), and *Bombus pascuorum* workers collected from a wild colony in Germany the same year had symptomatic DWV, which was the first evidence for this parasite in bumblebees (Genersch et al., 2006). Deformed wing virus is highly prevalent and usually asymptomatic in honey bees, but high intensity infections (normally related to vectoring by ectoparasitic *Varroa* mites) can cause physical deformities, inability to fly and possible colony collapse (Highfield et al., 2009). In bumblebees, controlled inoculation experiments have shown that DWV can reduce survival (Fürst et al., 2014; Graystock et al., in press). In 2007 and 2008, sampling of wild pollinators across England for a range of parasites detected DWV in wild *B. terrestris* and *B. pascuorum* bumblebees, *Vespula vulgaris* wasps and honey bees (Evison et al., 2012). Wild bumblebees across Great Britain and the Isle of Mann have DWV and *N. ceranae* at varying levels which mirror the prevalence of these parasites in local honey bees, with higher infection intensities in honey bees suggesting they may be the infection reservoir and that the parasites spillover to bumblebees (Fürst et al., 2014). Further analysis of these samples also identified BQCV, ABPV, SBPV and SBV in several sympatric bumblebee species and these too were associated with their prevalence in managed *A. mellifera* populations, further indicating spillover, spillback and/or parasite facilitation between populations of bumblebees and honey bees (McMahon et al., 2015). However, infection intensities of ABPV and SBV were greater in *Bombus lapidarius* and *B. hortorum* than in honey bees suggesting either spillover from bumblebees to honey bees, bidirectional spillover and spillback, or that intensity is influenced by host tolerance and life–history parameters too much to be an adequate predictor of transmission direction (McMahon et al., 2015; Runckel et al., 2011). It is in general now unclear whether viruses such as DWV which were first reported as honey bee pathogens are ancestrally honey bee pathogens that have subsequently jumped host into other bees, or whether the viruses ancestrally had a much greater host range than was previously realised, and have been traditionally considered as honey bee pathogens somewhat erroneously.

10. Conclusion

The balance of evidence suggests clearly that managed bees can, and have, had negative effects on wild bees, through parasite spillover, spillback and facilitation. Bumblebee colonies, which were commercially produced and imported into multiple countries over the last three decades, carried multiple infectious parasites with them, and the occurrence of parasites in managed colonies of honey bees is of course well known. The striking associations between the use of managed bees and local declines and extinctions of wild bees suggest strongly that multiple instances of parasite spillover, spillback and facilitation have occurred between managed and wild bees (Figs. 3–5). While the production of managed bees can be artificially increased to compensate for this, wild bee populations have to naturally bounce back, which may not be possible for many (Goulson and Hughes, 2015; Whitehorn et al., 2011).

Parasites have been found unequivocally in commercial bumblebees of several different species or subspecies, in three different continents, and from multiple suppliers, so disease appears to be a universal problem to commercial bumblebee breeders and their bees. Releasing managed bees therefore places wild bees at risk. Even when bees are reared in the same country of release, they could still introduce parasites to wild bees from the rearing facility. If it was possible to maintain disease free facilities, food and bees, the artificial introduction of large densities of disease free bees still may result in parasite spillback and parasite facilitation, and reduce the health of wild bees. Increased pollinator density has been suggested as a cause behind *B. terrestris* suffering increased disease prevalence in urban verse rural areas (Goulson et al., 2012).

Regulations regarding bumblebee screening are either absent in some territories or inadequate, such as European law Council Directive 92/65/EEC, which ensures bumblebees imported from 1992 must not show signs of American foulbrood (AFB) disease and must have no suspicion of *Tropilaelaps* mite or small hive beetle infestation. All three of these organisms are known predominantly for their harm to honey bees and are not considered a risk to bumblebees. The diversity of harmful parasites in bumblebees is far greater than previously considered yet most regulations regarding bumblebee screening have yet to acknowledge this.



Dates	Main events	Descriptions
1991	On Sale	*B. terrestris* imports sold
1996		*Nosema* detected in managed hives
1996		Naturalisation of *B. terrestris*
1998	On sale	*B. Ignitus* imports sold
1997-1999		Spillover of Japanese *Locustacarus buchneri* mite to *B. terrestris*
2000-2001		Spillover of *Locustacarus buchneri* mites in both directions

Fig. 3. Overview of parasite detection in managed bees in Japan and likely instances of parasite transmission between managed and wild bumblebees.

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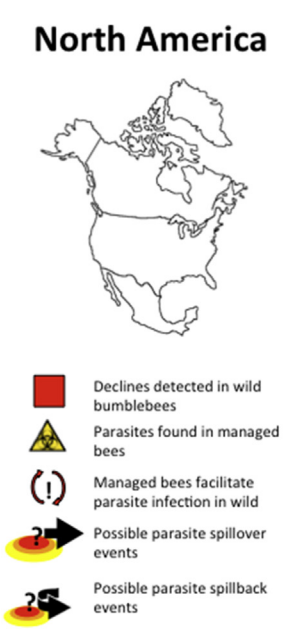
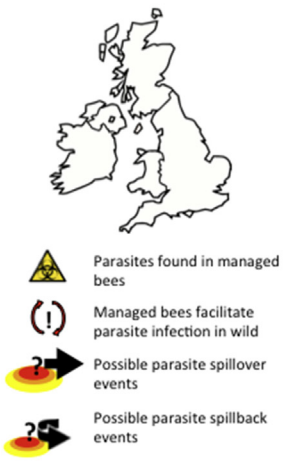


Dates	Main events	Descriptions
1992	On Sale	*B. occidentalis* & *B. impatiens* imported from breeding facilities in Europe
1994	Imports stop	Imports stopped, only bees reared in N. America can be used
1997		Managed *B. occidentalis* stocks reported to have high *Nosema bombi* prevalence
1997		Wild *B. occidentalis*, *B. affinis*, *B. pensylvanicus* and *B. terricola* decline
2002		*Nosema bombi* found in 51% of managed bumblebee colonies in one study
2004-2005		Wild bees nr farms using managed bumblebees had higher prevalence of *N. bombi* and *C. bombi*
2005		Proximity to farms using managed bumblebees predicted infections pattern of wild bumblebees with *C. bombi*
2007-2009		Declining Bombus species shown to have high *N. bombi* infections with likely European origin.
2008		DWV BQCV and IAPV found in *B. impatiens* from 2 suppliers
1980-2010		Meta analysis shows the rapid declines *of B. terricola* and *B. pensylvanicus* are likely to be the result of managed bumblebees
2014		45% sites tested with managed bumblebees have at least one of *L. buchneri*, *N. bombi*, *A. bombi*, DWV, IAPV, ABPV, CBPV or KBV

Fig. 4. Overview of parasite detection in managed bees in North America and likely instances of parasite transmission between managed and wild bumblebees.



Dates	Main events	Descriptions
1989	On Sale	Imports/release of *B. terrestris terrestris/dalmitinus* starts
2007-2008		Wild bumblebees found to have DWV, BQCV, ABPV, SBPV, SBV and *N. ceranae* at levels which mirror those of local managed honey bees
2008		74% of managed bumblebee colonies tested have *C. bombi*, *N. bombi* or *A. bombi*
2008		Wild bumblebees near farms using managed bees have higher infection rates than those not near managed bees.
2010		*C. bombi* infection dynamics differ in bees near sites using managed bumblebees in Scotland
2010	On Sale	Imports/release of *B. terrestris audax* starts
2011 -2012		77% of managed bumblebee colonies tested have *A. bombi*, *C. bombi*, *N. ceranae*, deformed wing virus, *Nosema apis* and *Nosema bombi*
2011		wild bees nr farms using managed bumblebees in England had higher prevalence of *A. bombi*, *C. bombi* and *N. ceranae*
2015	Release restrictions	The release of *B. terrestris terrestris/dalmitinus* heavily restricted.

Fig. 5. Overview of parasite detection in managed bees in the British Isles and likely instances of parasite transmission between managed and wild bumblebees.

For some wild bees, prevention of parasite spillover, spillback, and facilitation is too late. There are lessons to be learned, however, about the dangers associated with intensive management of pollinators. As bumblebees and other managed pollinators such as *Osmia spp.* are increasingly cultivated, these lessons will become ever more important.

10.1. Mitigating the harmful effects of managed bees on wild bees

There are a number of ways in which the harm managed bees cause to wild bees can be reduced. Firstly, parasites within rearing facilities must be prevented. A Likely route by which managed bumblebees come into contact with parasites is via the pollen (collected by managed honey bees) that the bumblebees are reared on (Goulson, 2013). Many known bee pathogens are transmittable via ingestion (Schmid-Hempel, 1998) and pollinator parasites including *C. bombi*, *N. bombi*, *N. apis*, *N. ceranae*, *A. bombi*, DWV, BQCV, SBV, *Ascosphaera* (chalk brood) and *Paenibacillus larvae* (American Foul brood) have all been found in honey bee pollen with several shown to be infective (Chen et al., 2006; Flores et al., 2005; Graystock et al., 2013b; Higes et al., 2008; Singh et al., 2010). Gamma irradiation of pollen has been shown to reduce the pathogenicity of the honey bee virus IAPV and two commercial bumblebee producers (Biobest, Westerloo, Belgium; Koppert, B.V., Berkel en Rodenrijs, The Netherlands) are known to have started treating their pollen this way in Europe (Meeus et al., 2014). Feeding bumblebees without introducing known (or unknown) parasites is an area in need of further research. Also, some bumblebee rearing facilities still mix honey bee workers in with bumblebee queens to encourage egg laying. Forcing these 2 species

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to live together provides an environment, which promote spillover to queens, which will later sire colonies that interact with wild bees. Further research into the production of colonies that doesn't rely on such practices are encouraged.

Exotic parasite introduction via the presence of exotic host species poses a particular risk; so controlling such exotic host introductions is a second mitigation measure that can be taken. In Japan, the non-native *B. terrestris* was added to a list of invasive alien species, prohibiting importation unless permits had been obtained by the farmer and they can prove no escapes are possible (Goka, 2010; Reade et al., 2014; Yoneda et al., 2007). In North America, importation of the non-native *B. terrestris* is banned outright (Winter et al., 2006), and in the UK the importation of non-native subspecies of *B. terrestris* is heavily restricted. Molecular screening is essential to identify the origin of many parasite strains and until done more thoroughly across various sites, the true identification of parasite spillover or spillback cannot be discerned. In cases when parasites are found upon delivery of managed bees, it seems likely to be spillover to wild bees, but a clearer understanding would be beneficial.

One of the best ways to avoid the potentially devastating effects of spillover, spillback, and facilitation in wild bees is to prevent their mixing with managed bees (Daszak et al., 2000; Foufopoulos et al., 2002). Farmers in many countries are now encouraged to use mesh on glasshouse windows or queen excluders on the front of hives to reduce the escape of commercially produced bumblebees. Despite this encouragement, studies have identified wild bees foraging inside glasshouses (Kraus et al., 2010; Lye et al., 2011a), and managed bumblebees foraging outside their glasshouses (Morandin et al., 2001; Murray et al., 2013). This population mixing results in the shared use of flowers by managed and wild bees, which are potential sites for parasite transmission (Durrer and Schmid-Hempel, 1994; Graystock et al., 2015; Singh et al., 2010). This highlights the ease with which wild and managed populations can mix and transmit parasites amongst themselves.

Based on this, we encourage the following to mitigate future and continued harm to wild bees:

- Strict, unified international regulations are needed to ensure bee movements do not introduce exotic parasites to new countries.
- Improved screening for a wider range of parasites, particularly cryptic viral infections.
- Improved husbandry to eliminate parasites within rearing facilities.
- Improved barrier control on farm glasshouses and poly tunnels to avoid mixing between managed and wild bees.
- Increase hedgerows and wildflower field margins to increase wild pollination services and reduce reliance on managed bees.
- Increased conservation effort to small/fragmented wild bee populations that are under increased stress.

While this will undoubtedly impose short-term monetary costs, it will help to protect wild bees and the valuable pollination services they provide in the long term. For honey bees, barrier control is however impossible so practices will instead rely heavily on regular screening and mitigative actions upon disease discovery, including the prevention of further movement by diseased hives. In the case of bumblebees used in glasshouses, complete barrier protection is possible and is a success story in Japan where regular parasite screening is also performed as a second line of defence (Reade et al., 2014).

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